AN ENDOGENOUS DIURNAL RHYTHM OF BIOLUMINESCENCE IN A NATURAL POPULATION OF DINOFLAGELLATES[1]

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Several authors have shown or suggested that dinoflagellates are the major source of bioluminescence in many surface regions of the ocean (Backus, Clark and Wing, 1965; Backus, Yentsch and Wing, 1961; Gold, 1965; Hardy and Kay, 1964; Seliger *et al.*, 1961, 1962; Sweeney, 1963; Yentsch, Backus and Wing, 1964; earlier work summarized by Harvey, 1952, p. 124). Hastings and Sweeney (1957, 1958) and Sweeney and Hastings (1957) have studied an endogenous diurnal rhythm of light production in laboratory cultures of the dinoflagellate *Gonyaulax polyedra*. Earlier work summarized by Harvey (1952, p. 128) has suggested an endogenous rhythm in flashing, but lack of dark-adaptation of the observer makes these reports questionable. Harvey (1952, p. 129) reports a more careful experiment but in an abnormally eutrophic environment. None of these reports give quantitative measurements, and none of these compare the endogenous influences with the exogenous influence of light inhibition.

An *in situ* diurnal rhythm of luminescence within the euphotic zone, probably caused by dinoflagellates, has been found by Backus *et al.* (1961) and Clarke and Kelly (1965), although this rhythm has not been shown to be endogenous. Other workers have found an *in situ* rhythm and concluded that it was exogenous in origin. Seliger *et al.* (1961, 1962) postulated that the rhythm was controlled by a diurnal migration of the luminescent dinoflagellates. Yentsch *et al.* (1964) pointed out that photo-enhancement and photo-inhibition alone might explain the amount of bioluminescence and that diurnal migration was not involved. Backus *et al.* (1965) found that bioluminescent organisms in Eel Pond responded to the eclipsing sun much as they normally respond to the setting sun, and that their behavior from mid-eclipse to eclipse end resembled dawn behavior. They concluded that the exogenous factor of changing light overrides such endogenous rhythms as may exist.

The purpose of the work reported here was to resolve the relative importance of endogenous and exogenous influences on the diurnal rhythm of bioluminescence of a natural population of phytoplankton under controlled conditions, and to identify the members of the population responsible for the luminescence in a typical inshore marine environment.

Methods

Surface water was taken at various times of day from near the entrance to Eel Pond—a salt pond in Woods Hole, Mass., which is tidally flushed by water from

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the connecting harbor, and which has phytoplankton populations similar to those in the harbor. This water was filtered through 0.33-mm. aperture netting, and placed in a Teflon-lined 15-gallon steel drum. The contained organisms were stimulated by controlled air flow from an aquarium bubbler "stone" placed near the bottom, and bioluminescence was measured using a photomultiplier photometer with logarithmic output and sensitive to intensities as low as 10^{-8} μw./cm.^{2}. The photometer window was in the water 8 cm. above the bubbler, and the output was recorded on a Sanborn strip-chart recorder with 0.01 second response time. Organisms were stimulated for 40 to 60 seconds at various times depending on the particular experiment and flashing was recorded during stimulation. Total flashes were counted for the first 30 seconds of stimulation, and bioluminescence expressed as flashes/30 seconds. This measurement was used rather than total light output since amount of flashing is an ecologically more meaningful quantity, and since it was impossible to know the number of organisms subject to stimulation. Stimulation provided sufficient mixing to prevent stratification of the organisms. All experiments were performed in a darkroom at temperatures between 20° and 22° C.

Experiments

Three types of experiments were performed. The first measured the endogenous luminescence rhythm by recording luminescence of populations kept continually in darkness. The second studied the recovery of ability to luminesce when populations taken from normal daylight in the natural environment were placed in darkness. The third group of experiments measured the effects of exposure to light at various times of day on the luminescence of populations kept in darkness.

In the first experiment, water was collected, filtered, and placed in complete darkness in the laboratory just prior to 1900, 16 Aug., 1965, and stimulated flashing was recorded every hour from 1900 until 0300, 20 Aug., 1965. Flashes/30 sec. are plotted against time in Figure 1. An endogenous rhythm of flashing rate was apparent and continued for three days, although the maximum flashing rate was lower each day. A similar experiment was performed between 3 Aug. and 5 Aug., 1965, and although the recording methods were different, the results were qualitatively the same. These results are qualitatively similar to those found by Sweeney and Hastings (1957) who measured total light output by cultures of *Gonyaulax polyedra*. The changes in flashing rate are also similar to *in situ* measurements made by Backus *et al.* (1961) except that the morning decrease and evening increase in flashing are not as pronounced in the present work.

In order to study recovery from inhibition due to daylight, two series of experiments were performed in which water was brought from the surface of Eel Pond into complete darkness at various times of day (daylight intensities from 5×10^4 to 1×10^5 μw./cm.^{2}, measured with a General Electric photoelectric meter). Flashing rates were recorded every hour thereafter until 2300. The two series gave similar results, and the results of the second series and the times of start of dark exposure are shown in Figure 2. Rates of flashing throughout the day of organisms in continuous darkness are shown for comparison (results of Aug. 30 experiments; see below and Figure 3).

Flashing rates in water collected during daylight increased within two hours to the rate shown by a population kept in darkness for the previous night, and

then followed the curve for that population. Flashing rates in water taken at night were initially much higher. Thus, inhibition of flashing by daylight superimposes its effect upon a daytime decrease controlled by an endogenous rhythm. This is further emphasized in the next group of experiments.

The third group of experiments examined the effects of inhibition by exposure to short periods of artificial light at various times of day. On three occasions water was brought into the darkroom at dusk (2000) and the included organisms were allowed to dark-adapt until midnight. They were then exposed to 15 minutes of light every two hours for 24 hours and luminescence was recorded 15, 30, 45, 60, 90 and 120 minutes after start of light exposure. Intensities at the surface of the water, dates, and certain minor departures from the described schedule are shown in Figure 3. The lower surface light intensity at 1470 μw./cm.^{2} was provided by

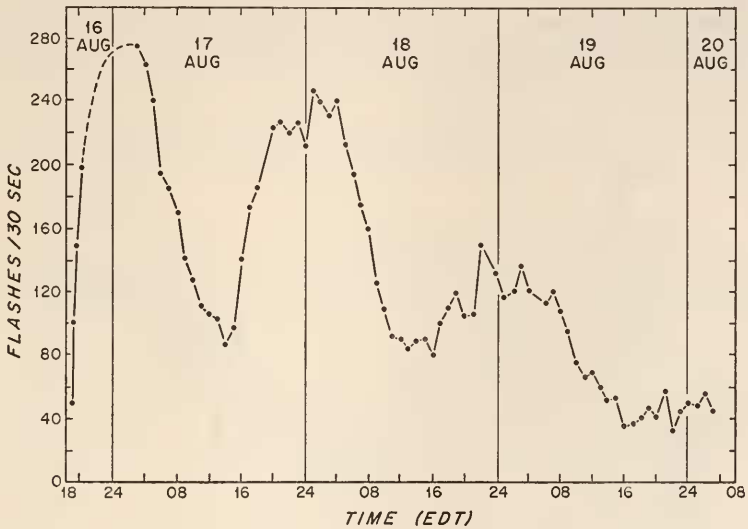

FIGURE 1. Flashing rates during stimulation for 30- to 60-second duration recorded in water collected at 1900 hr. 16 Aug. 1965 and kept continuously in the dark for the period shown.

placing over the barrel a bank of fluorescent lamps, rated by the manufacturer to have a spectral distribution similar to normal daylight. The higher light intensity of 8820 μw./cm.^{2} was provided by an incandescent spotlight which had a different spectral distribution and angular dispersion. Light intensity was attenuated by about 30% through a 60-cm. water layer in Eel Pond, and probably by a similar amount in the barrel. The rising air bubbles used for stimulation mixed the water and assured random dispersal of the organisms with uniform exposure to light.

Results of these experiments are shown in Figure 3. The lower curves connect the flashing rates after 15 minutes of light exposure, and the upper the rates after active recovery from light inhibition had apparently stopped (1 hr. 45 min. after exposure). Although the figures differ somewhat, presumably because of population changes, they are all similar in that they show proportionately greater inhibition

during daylight hours. Since the treatment and environmental conditions were the same both day and night, it may be concluded that there is an endogenous diurnal rhythm in sensitivity to light inhibition. The similarity of the flashing rates after recovery from light inhibition to those of populations kept in continuous darkness indicates that there is no appreciably long-term effect of light exposure.

The two intensities used are approximately equivalent to 2% and 12% of the mid-day surface light intensity in Eel Pond. Although the higher intensity of 8820 μw./cm.^{2} caused slightly greater inhibition, the flashing was never reduced by more than $\frac{2}{3}$. Sweeney, Haxo and Hastings (1959) noted that exposure of *G. polyedra* cultures to light caused inhibition of luminescence to varying degrees, depending on the intensity of the light, and that longer exposure to light altered the phase of the rhythmicity. They did not, however, mention significant variations in sensitivity to inhibition with time of day. The lack of a phase shift in the present experiments was probably due to the relatively short exposure and low intensity. Many luminescent marine organisms are known to be inhibited by light (Harvey, 1952), but only dinoflagellates and euphausids (Mauchline, 1960) are known to have

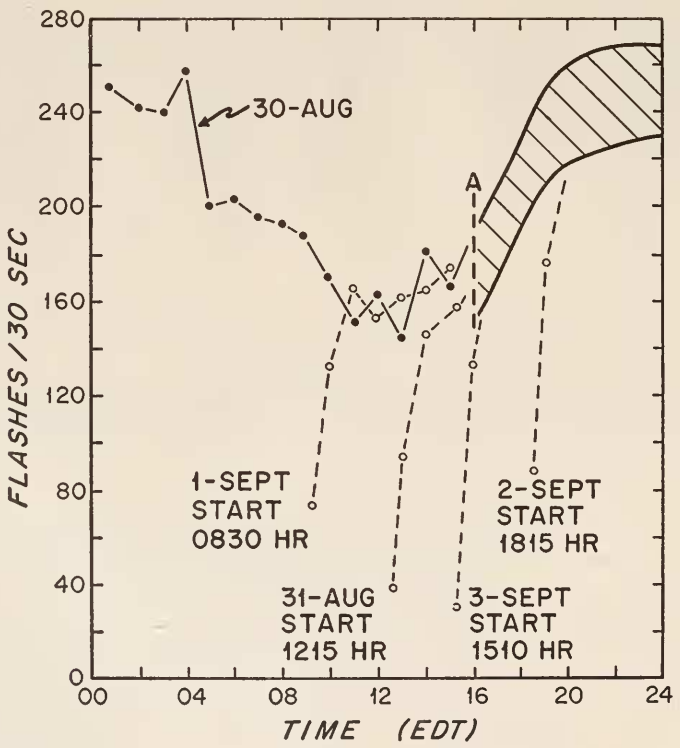

FIGURE 2. Flashing rates recorded using water collected from the natural environment at dates and times shown, and placed immediately in darkness. After time "A" (1600 hr.), all flashing rates fell on approximately the same curve, and only the range of flashing rates is shown by the cross-hatched area.

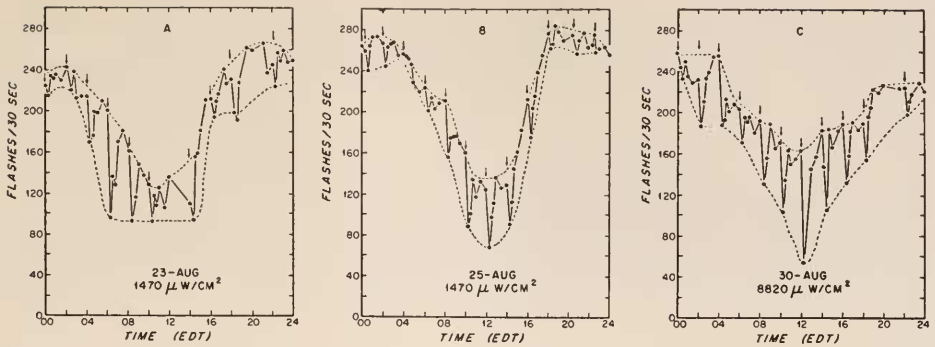

FIGURE 3. Effect of light inhibition at various times of day. Dates, times, and light intensities as shown. Times of start of light exposure for 15 minutes are indicated by arrows. Upper dashed line connects rates after complete recovery; lower line connects rates after light exposure.

an endogenous rhythm in flashing activity, and there are no reports known to us of an endogenous variation in sensitivity to light inhibition.

DISCUSSION

These experiments with natural populations brought into the laboratory attempt to bridge the gap between the studies of luminescence in cultured dinoflagellates made by Hastings, Sweeney, and co-workers, and the previous field studies in which rhythms in dinoflagellate luminescence were found (references in the introduction). Our results indicate that the flashing rates of populations kept in darkness decrease during daytime hours, and that the effect of light in causing inhibition of flashing is greater during daytime. Both the dark-adapted flashing rates and the sensitivity to photo-inhibition are controlled by an endogenous diurnal rhythm.

Hastings and Sweeney (1958) found an endogenous rhythm in the effect of periods of light exposure on changing the phase of the luminescence rhythm. Their effect had a maximum sensitivity during dark hours in contrast to the varying sensitivity to light inhibition found here, which has a maximum during daylight. It may be inferred from this that unless the experimental organisms vary, different mechanisms are involved in these two manifestations of light sensitivity.

Hastings and Sweeney (1958) also found a greater night-day variation in light production than is found here. This is probably because they measured total light output rather than number of flashes. Since in their experiments the intensity as well as rate of flashing was greater at night, total light output increased to a greater extent. This night-time increase in intensity was not apparent in our records.

Because the light-inhibition effect is the most obvious with *in situ* measurements, several of the authors mentioned in the introduction have considered control of flashing to be only exogenous, but this is apparently an oversimplification. Yentsch *et al.* (1964) found that a model involving only photo-enhancement and photo-inhibition described the diurnal variation, but it appears that this is useful only as an empirical approximation. Seliger *et al.* (1961, 1962) have hypothesized diurnal

migration as the cause of variation in light production, but this appears to be neither sufficient nor necessary to explain the variations we observed.

Backus *et al.* (1965) have described the effect of a solar eclipse on luminescent activity to be similar to that of the setting sun, and they concluded that the exogenous factor of changing light overrides such endogenous rhythms as may exist. Experiments described above, however, showed that populations brought into darkness from complete daylight in the natural environment increased their flashing rate only by an amount determined by the diurnal rhythm and not to a night-time level. If the dark period of the eclipse had been longer, recovery from inhibition might have been complete, and it might have become apparent that light-inhibition of flashing rates is not the only cause of the daytime decrease in flashing rate.

Bode, DeSa and Hastings (1963) and Hastings and Keynan (1965), using *G. polyedra* cultures, have shown that normally more luciferin is produced at night than during the day. This was inferred because if night-time flashing was inhibited by temperature or light, more luciferin could be extracted at that time. Under normal conditions, however, night-time flashing apparently utilizes the available luciferin, and more is extracted during the day when flashing is less. It thus appears light inhibition does not affect substrate production, but rather acts upon the stimulus-response mechanism; *i.e.*, it probably decreases the sensitivity of the cells to stimulus. This suggests that flashing of natural populations may be controlled both by the availability of luciferin and by light-inhibition of the sensitivity to stimulus.

The selective advantage conferred upon a dinoflagellate by its ability to luminesce and to control the amount of luminescence is undetermined. McElroy and Seliger (1962) have hypothesized that luminescence first developed to serve a biochemical function during the early evolution of life. As presently found in dinoflagellates, however, the biochemical ability for luminescence is accompanied by at least three mechanisms that serve to control the output of light: (1) a sensitivity to stimulus and an associated effector system, (2) a mechanism whereby sensitivity to stimulus is controlled by light inhibition, and (3) an endogenous rhythm in luciferin production. Energy is required for the production of light, and it seems unlikely that a complex energy-requiring system such as this would evolve and not be lost in such a diverse and widespread group of organisms unless some selective advantage is conferred upon the organisms. More work on the behavior and ecology of luminescence in dinoflagellates is necessary to detect any such advantage.

Although many marine organisms are known to be less luminescent during the day than at night (Harvey, 1952), the only one other than dinoflagellates which has been shown to have an endogenous rhythm is the euphausid shrimp *Meganyctiphanes norvegica* (M. Sars) (Mauchline, 1960). It apparently increases its flashing rate at night even after being kept in the dark for two days. Since the animal has complex photophores with neural and muscular control, presumably luminescence is important in its behavior.

In addition to endogenous and exogenous influences on the luminescence of species of dinoflagellates within a population, luminescence in the natural environment may vary because the species present change and exhibit different characteristics. *G. polyedra* and *Gonyaulax monilata* display similar endogenous rhythms,

whereas *Noctiluca miliaris* gives no indication of an endogenous rhythm (Hastings, 1959). More must be known of the behavior of individuals and cultures of various species before any model can be proposed to describe the behavior of a population composed of many species.

Determinations of Luminescent Species

In order to determine which species of dinoflagellates present during the experiments were capable of luminescence, individual specimens of the species predominant during August and September, 1965, were isolated from the plankton and tested.

Tows were taken on several afternoons, using a nylon net with 35 μ mesh aperture. Water passed through the same net was found to be not luminescent, and it is assumed that all luminescent forms of phytoplankton were captured. Representatives of the dinoflagellates were removed from the sample by micropipette, placed in filtered sea water, and motile individuals were transferred singly from this into 0.5 ml. of filtered sea water in test tubes. The organisms in tubes were kept in the dark until after 2100 hr. before they were tested, so that potential for luminescence would be high when tested, and so that the organisms could recover from the isolation procedure.

The tubes were placed in a light-tight holder in front of the photometer that was used in the previous experiments, and air was bubbled through the water to stimulate the organisms. After testing, the contents were examined to determine if the organisms were still motile, and only those which were motile or which had flashed were considered to have been alive during testing and only these are included in the results. The organisms were placed in a drop of filtered sea water on a slide in a moist petri dish and left overnight. This killed the organisms and often resulted in a loss of protoplasm that simplified drawing and identification.

The organisms tested were drawn with a camera lucida, and were usually placed in glycerine-jelly to facilitate handling and determination of plate structure. Drawings were then compared with more thorough drawings made of specimens of the same species that were not tested, but which were more easily cleared, stained, and manipulated without risk of loss.

Although cell counts of dinoflagellate population density were not made, it was apparent that the populations varied somewhat from day to day. Dinoflagellates were greatly outnumbered by diatoms, but the latter have never been found to be luminescent (Sweeney, 1963). Larger forms which might have been luminescent (such as copepods and ctenophores) had been excluded by filtration. Radiolarians may be luminescent, but were present in very small numbers.

The results of the tests are shown in Table I. Because cells that had been tested were often difficult to recover for identification, only those individuals definitely identified have been included in the table. For example, at least 10 specimens of what was tentatively identified as *Gonyaulax digitale* were tested, and most were luminescent, but were not recovered after testing. Very few of the tested *G. spinifera* flashed, and few were examined for motility after testing. Several specimens of *Gonyaulax* and *Peridinium* believed to be of different species than those identified were examined and were luminescent, but were not identified owing to the lack of specimens. These are listed as *spp.* in Table I.

Of the 12 species and four genera of dinoflagellates present in the Eel Pond plankton during August and September, 1965, 10 species were found to be luminescent. These included the vast majority of dinoflagellate individuals present, and certainly were primarily responsible for the recorded bioluminescence. Of the species found to flash, the following have been previously reported as luminescent: *Peridinium conicum* (Sweeney, 1963), *P. granii* (Ganapati *et al.*, 1959), and *Ceratium fusus* (Lebour, 1925; Sweeney, 1963). Sweeney (1963) tested *P. claudicans* by a similar method and found it not to be luminescent. *Ceratium tripos* has been reported by several authors to be luminescent (Sweeney, 1963), but neither Sweeney nor the present authors could demonstrate a luminescence.

TABLE I

Results of testing individual dinoflagellates for bioluminescence

Species	Number of cells that flashed	Number of motile cells that did not flash
Gonyaulax digitale	2	0
G. spinifera (see text)	2	Several
Gonyaulax spp.	(see text)	
Glenodinium lenticula	0	10
Peridinium claudicans	2	1
P. conicum	2	0
P. granii	4	0
P. leonis	4	0
P. oceanicum	2	0
P. subinerme (Var. *punctulatum*)	4	0
Peridinium spp.	(see text)	
Ceratium fusus	2	3
C. lineatum	0	10
C. tripos	0	12

The present study has therefore added 6 species to the list of dinoflagellates known to be luminescent.

Negative results in tests such as these must not be considered conclusive, since an organism such as *P. claudicans* or *C. tripos* may sometimes flash and sometimes not. Thus, there appear to be some species always capable of luminescence, some that never luminesce, and others which are capable of luminescence only under certain conditions.

TAXONOMY

No thorough taxonomic work has been done on the armored dinoflagellates of the region directly south of Cape Cod, and identification must be made with reference to Lebour (1925) and Schiller (1937), who deal primarily with European and oceanic forms. The species referred to as *Glenodinium lenticula* (Bergh) Schiller, and several species of *Peridinium* are in need of revision. It is deemed desirable to illustrate and note the characteristics of the five species given below so that our identification will be meaningful in case of future revision. The other species tested seem secure in their taxonomic position.

Glenodinium lenticula (Bergh) Schiller (Fig. 4, g–j).

This species is very variable and has a lengthy synonymy (Schiller, 1937). The form worked with here varies considerably within the population. It may have four apical plates; *i.e.*, a plate that some authors have described as the second intercalary (Schiller, 1937, p. 104; Figs. 95, 96) actually reaches the apical pore. Individual specimens may or may not have a small asymmetrical intercalary plate between precingulars 2″ and 3″ and apicals 2′ and 3′. Schiller (1937) illustrates forms with and without this plate. If this plate is not present, there are 7 precingulars, the third reaching further toward the apex in place of the asymmetrical intercalary; if the intercalary is present, only 6 precingulars are found. The widths of the pre- and postcingular plates are very variable, and in some cases these plates are barely visible. The theca is punctate, the sutures are often broad and striated, the lists have very fine supporting spines, and the apical pore may or may not be strongly developed. Plate structure of the species described here: 4 apicals, 0 to 1 intercalary, 7 or 6 precingulars, 5 postcingulars, and 2 antapicals.

Peridinium conicum (Gran) Ostenfeld and Schmidt (Fig. 4, d–f).

In the past this species has been confused with both *P. pentagonum* Gran and *P. leonis* Pavillard, and the differences between them are slight. Lebour (1925, p. 111) and Schiller (1937, p. 237) separate *P. pentagonum* from *P. conicum* on the basis that the former has solid antapical spines, and that its right half is larger than its left, but this is not shown clearly in their figures. These characters are nevertheless sufficient to identify the species discussed here.

Peridinium leonis Pavillard (Fig. 4, k–n)

This species is easily separated in our samples from the previous one although earlier descriptions (Schiller, 1937, p. 236) indicate a wide variation. It may be distinguished from other species described here by the following characters: cell dorso-ventrally flattened, broad lists with prominent spines, girdle forms an acute angle with cell axis, surface with reticulations appearing striated on some plates, first apical plate narrower than in *P. conicum*. Schiller (1937, p. 236) and Lebour (1925, p. 112) have separated it from *P. conicum* on the basis of its much more prominent lateral sutures, but this is not always evident in the individuals investigated here. The species here corresponds most closely to those described by Dangeard (1927) and Klement (1964), and probably several similar species are included in *P. leonis* in the summary by Schiller (1937).

Peridinium granii Ostenfeld (Fig. 4, a–c).

This species is easily confused with *P. brochii*. The only character separating them is the asymmetry of the dorsal plate structure, and this is variable (Schiller, 1937, p. 189). It is easily separated from the other species investigated here, however, by the structure of the first apical plate. The present form corresponds most closely to that illustrated in Lebour (1925, p. 124). It is characterized by the structure of the first apical plate and the asymmetry of the dorsal plates.

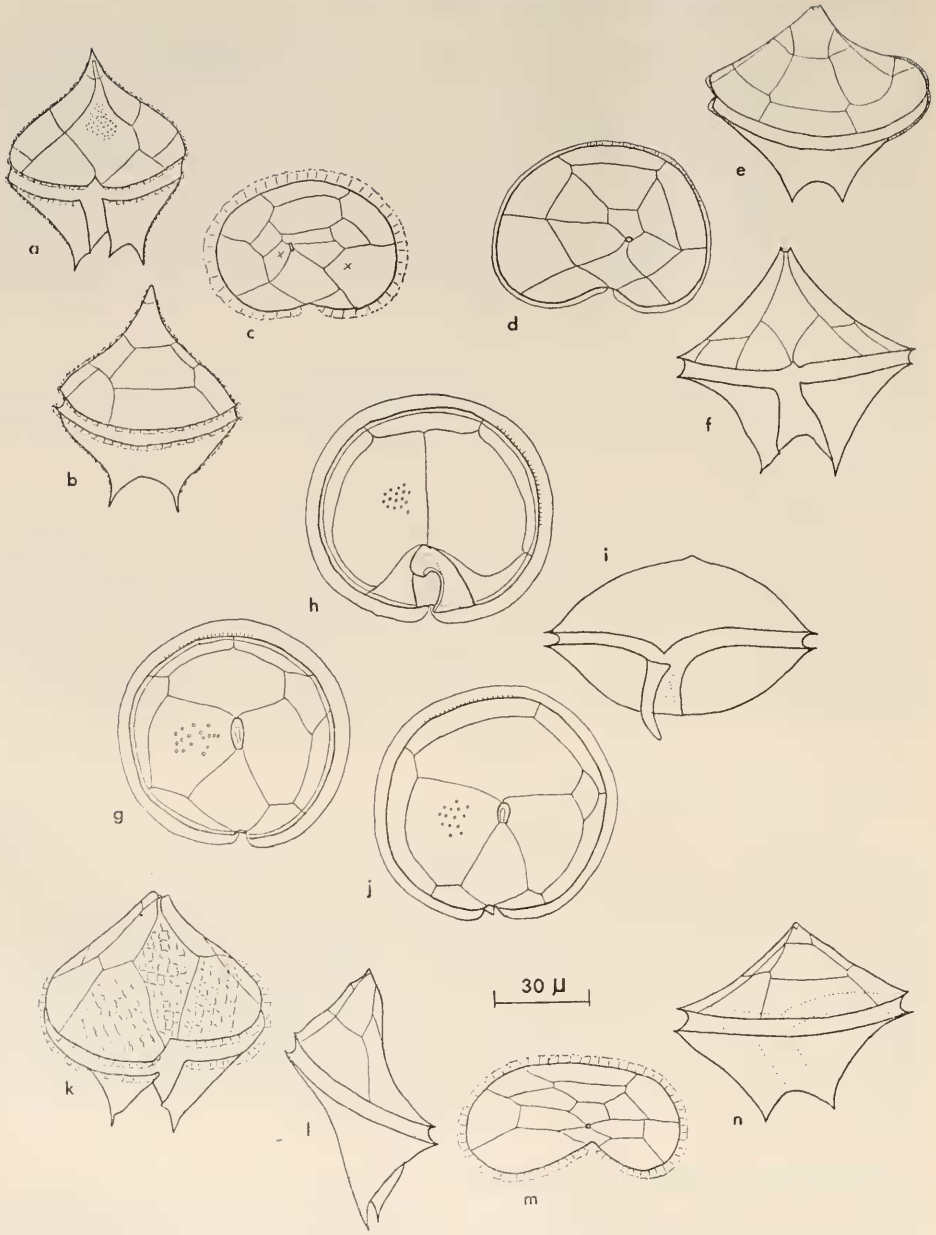

FIGURE 4. Dinoflagellates whose taxonomy is discussed in text. a–c, *Peridinium granii;* d–f, *Peridinium conicum;* g–j, *Glenodinium lenticula;* k–n, *Peridinium leonis.*

Conclusions

Most dinoflagellate species and individuals taken from Eel Pond during this study were luminescent and these were sufficient in abundance to explain all the luminescence recorded. This is probably the case in many marine environments. Macroscopic organisms capable of luminescence were removed by filtration, and the only microplankton constituents capable of luminescence and present in sufficient numbers were dinoflagellates.

Dinoflagellate luminescence is commonly a cause of light production in surface regions of the ocean (Harvey, 1952; Hastings, 1963) and more knowledge is needed of the luminescent behavior of individuals and cultures of the various species. The effects of temperature, depth and other environmental conditions are unknown. Spontaneous luminescence without stimulation was observed in the laboratory, but is very variable and its extent in the natural environment is not known. Much work is needed on the ecology of dinoflagellate luminescence.

The rate of luminescent flashing of natural populations following stimulation is greatest at night, is controlled by an endogenous diurnal rhythm, and is inhibited by light. The sensitivity to light-inhibition is also controlled by an endogenous rhythm, and is greatest during midday when flashing is least. Thus in the natural environment, light-inhibition and an endogenous rhythm act together in decreasing stimulated daytime luminescence.

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